NeoBiota 65: 47–69 (2021)
doi: 10.3897/neobiota.65.63179
https://neobiota.pensoft.net

RESEARCH ARTICLE

A peer-reviewed open-access journal
NeoBiota
Advancing research on alien species and biological invasions

Competitive ability of native and alien plants: effects of residence time and invasion status

Christine S. Sheppard[1], Marco R. Brendel[1]

1 *Institute of Landscape and Plant Ecology, University of Hohenheim, 70593, Stuttgart, Germany*

Corresponding author: Christine S. Sheppard (christine.sheppard@uni-hohenheim.de)

Academic editor: José Hierro | Received 18 January 2021 | Accepted 30 March 2021 | Published 25 May 2021

Citation: Sheppard CS, Brendel MR (2021) Competitive ability of native and alien plants: effects of residence time and invasion status. NeoBiota 65: 47–69. https://doi.org/10.3897/neobiota.65.63179

Abstract

Competition is commonly thought to underlie the impact of plant invasions. However, competitive effects of aliens and competitive response of natives may also change over time. Indeed, as with time, the novelty of an invader decreases, the accumulated eco-evolutionary experience of resident species may eventually limit invasion success. We aimed to gain insights on whether directional changes in biotic interactions over time or more general differences between natives and aliens, for instance, resulting from an introduction bias, are relevant in determining competitive ability. We conducted a pairwise competition experiment in a target-neighbour design, using 47 Asteraceae species with residence times between 8 years-12,000 years in Germany. We first tested whether there are differences in performance in intraspecific competition amongst invasion status groups, that is casual and established neophytes, archaeophytes or native species. We then evaluated whether competitive response and effects depend on residence time or invasion status. Lastly, we assessed whether competitive effects influence range sizes. We found only limited evidence that native target species tolerate neighbours with longer potential co-existence times better, whereas differences in competitive ability were mostly better explained by invasion status than residence time. Although casual neophytes produced most biomass in intraspecific competition, they had the weakest per-capita competitive effects on natives. Notably, we did not find differences between established neophytes and natives, both of which ranked highest in interspecific competitive ability. This lack of differences might be explained by a biased selection of highly invasive or rare native species in previous studies or because invasion success may result from mechanisms other than interspecific competitive superiority. Accordingly, interspecific per-capita competitive effects did not influence range sizes. Further studies across a broader range of environmental conditions, involving other biotic interactions that indirectly influence plant-plant interactions, may clarify when eco-evolutionary adaptations to new invaders are a relevant mechanism.

Copyright *C. S. Sheppard, M. R. Brendel.* This is an open access article distributed under the terms of the Creative Commons Attribution License (CC BY 4.0), which permits unrestricted use, distribution, and reproduction in any medium, provided the original author and source are credited.

Keywords
Asteraceae, biotic interaction, co-existence time, competition experiment, competitive response and effect, eco-evolutionary experience, introduction bias, plant invasion

Introduction

Biological invasions are a major driver of global change, posing a threat to native species, communities and ecosystems (Simberloff et al. 2013; Pyšek et al. 2020). For plant invasions, competition is the most commonly invoked mechanism by which alien species impact natives (Levine et al. 2003). Understanding whether alien species benefit from higher interspecific competitive ability and whether the resulting local dominance is linked to large-scale invasion success, is thus crucial for conservation management. According to Parker et al. (1999), an invader's potential impact is the product of abundance, per-capita effect and range size. It has long been suggested that locally-abundant species are generally also the ones that are widespread (Lawton 1993) and that rare species are competitively inferior (Griggs 1940). Accordingly, some studies have found that alien species with higher local interspecific competitive ability may also reach larger range sizes (Milla et al. 2011; Sheppard 2019), although other studies with native species have not consistently found such an effect (e.g. Lloyd et al. 2002). Additionally, performance in intraspecific competition may also be an important determinant of invasion success, given that alien species often dominate in dense monospecific stands.

Given its importance for invasion success and impacts, competition amongst aliens and natives has long been studied (Vilà and Weiner 2004). However, a neglected aspect of competition experiments, so far, is the possibility that competitive effects of aliens and competitive response of natives to aliens might change over longer timescales. As a result of eco-evolutionary changes following the introduction of a new species, the performance and potential impacts of an invader may depend on its residence time; that is, the time since introduction to a new area. In fact, one of the most consistent findings in invasion biology is the importance of residence time, particularly for increasing range sizes (Pyšek and Jarošík 2005; Williamson et al. 2009; Pyšek et al. 2015). Beyond affecting range sizes, residence time also has consequences for other ecological and evolutionary processes affecting the invader and resident plant communities (e.g. Lankau et al. 2009; Lankau 2011; Dostál et al. 2013; Gruntman et al. 2017). With increasing residence time, an invader may adapt to its new environment, such as to new climate conditions (Colautti and Barrett 2013), increasing population growth and spread. Conversely, as the novelty of an invader and of the biotic interactions between invader and resident competitors and antagonists decreases over time, the accumulated eco-evolutionary experience of resident species may eventually limit population growth and spread of invaders (Hawkes 2007; Saul et al. 2013; Sheppard and Schurr 2019; Germain et al. 2020).

As competition for limiting resources may act as a selection pressure, plants with a history of co-existence may have developed niche differentiation or reached a bal-

ance in competitive abilities through adaptive evolution (Thorpe et al. 2011). Hence, evolutionary changes in competitive ability with residence time may be important for long-term changes in invasion success. From the invader perspective, competitive effects may increase, for instance, when, due to a release from natural enemies, invaders invest less in defence and instead more in competitive ability (evolution of increased competitive ability hypothesis, Blossey and Nötzold 1995). In contrast, evolutionary responses of native species to invaders are less frequently considered and most evidence involves animals (Strauss et al. 2006). Thereby, high impacts of alien species are frequently explained by the native species being naïve with regards to the novel threat (which, however, can be overcome over time, for example, Bytheway and Banks 2019). The few studies investigating evolutionary adaptation to competition between plants have mostly focused on invasive plants that produce allelochemicals (Callaway et al. 2005; Lankau 2012; Dostál et al. 2013). In this regard, the novel weapons hypothesis posits that invaders may succeed because they have novel weapons to which native species are not adapted (Callaway and Aschehoug 2000). However, native species may also learn to tolerate such novel weapons over time, in which case they should show stronger competitive responses with length of co-existence time. For instance, native grasses growing for 20–30 years with *Centaurea maculosa* in North America, tolerate the allelochemicals better than native grasses of the same species from uninvaded habitats (Callaway et al. 2005). Overall, a meta-analysis of 53 comparisons from 14 experimental studies showed that experienced natives (plants from populations growing with the invader) had higher levels of growth and reproduction than naïve natives (plants from populations that have not yet experienced invasion) (Oduor 2013). Germain et al. (2020) recently demonstrated that such gained experience in a native annual grass, which led to increased competitive ability, can, in turn, reduce invasion growth rate of an invasive annual grass considerably.

Differences in competitive ability between invader and resident species are not necessarily only the result of such gradual directional changes in competitive interactions. Instead or additionally, there may be *a priori* differences in competitive ability that result from an introduction bias. This means that alien species are not a random sample of all plants of the world. Indeed, alien species tend to have a stronger human association and may, hence, be more adapted to human-modified environmental conditions (Buckley and Catford 2016). Furthermore, species deliberately introduced and grown for ornamental or horticultural purposes (which represent the majority of established alien plants in Europe, Lambdon et al. 2008) tend to be strong competitors or have a ruderal strategy, rather than being tolerant to stressful abiotic conditions (Guo et al. 2019). In contrast to the neophytes, the archaeophytes (alien plants introduced before Columbus' discovery of the Americas in 1492) are ruderal or segetal species, originating from drier and warmer regions of the Fertile Crescent and tend to be adapted to more extensive traditional land use (Chytrý et al. 2008; Zając et al. 2009). Such an introduction bias may thus result in *a priori* differences in competitive ability between native, neophyte and archaeophyte species. Indeed, meta-analyses have shown that invasive neophyte species possess traits that distinguish them from native species and

which may confer higher competitive ability (Ordonez et al. 2010; van Kleunen et al. 2010). Although generally fewer studies considered archaeophytes, they have been shown to differ in traits compared to natives (Knapp and Kühn 2012). Nevertheless, it has also been argued that common natives which are successful in human-disturbed habitats may display similar traits as alien species (Thompson and Davis 2011). The concept of discrete "invasion status" categories (such as casual, established, invasive aliens vs. natives, Blackburn et al. 2011) is often employed in invasion biology and can be helpful in highlighting such differences amongst groups because of an introduction bias. However, invasion status groups are sometimes also used as a proxy for effects of residence time. If these latter mechanisms are relevant, such discrete categories may, however, not fully account for directional changes during the process of biological invasions, whereby such eco-evolutionary mechanisms may be better described by residence time as a continuous gradient (Sheppard and Schurr 2019).

In this study, we aimed to gain insights into whether continuous residence time or categorical invasion status may explain differences in competitive ability between natives and aliens better and whether any such differences have consequences for large-scale invasion success (i.e. if species with higher competitive ability reach larger range sizes). Thereby, we specifically aimed to test if we find directional changes in competitive ability over time, consistent with an increase in biotic resistance of native species to newly-introduced species. Alternatively, we considered whether we rather find evidence for more general differences amongst invasion status groups, resulting either from an introduction bias or other non-directional eco-evolutionary processes. To this end, we conducted a pairwise competition experiment with 47 Asteraceae species along an "alien-native species continuum", including species along a continuous gradient of residence times (Sheppard and Schurr 2019) and also representing the four discrete invasion status categories of casual neophytes, established neophytes, archaeophytes and native species in Germany. Such multi-species experiments, although still rarely used in ecology, are very useful in searching for general patterns and mechanisms (van Kleunen et al. 2014). We studied pairwise competition of five native target species with 47 alien and native neighbour species, varying in residence times from 8 years to 12,000 years. This enabled us to assess whether tolerance (competitive response) of native species to competition from neighbours increases with their length of potential co-existence time, as expected if native species gain eco-evolutionary experience and increase biotic resistance to newly-introduced alien species. Additionally, given the potential importance of intraspecific competition for invasion success, we also assessed performance of each neighbour species.

Overall, we thus address the following research questions: 1) Does performance in intraspecific competition depend on invasion status? Note that in this first question we did not test for effects of residence time since no interspecific interactions were involved (i.e. no variation in potential co-existence times). 2) Does interspecific competitive ability (competitive response of five native targets and competitive effects of all 47 alien and native neighbours) depend on residence time or invasion status? 3) Do interspecific competitive effects (and residence time) influence range size?

Methods

Alien-native species continuum

Our study focused on 47 species of annual Asteraceae along an alien-native species continuum (Sheppard and Schurr 2019) (see Suppl. material 1: Fig. S1), representing species of increasing residence times between 8 years-12,000 years in Germany (including 10 casual neophytes, 15 established neophytes, 15 archaeophytes and 7 natives). We limited our study system to one family so that we could focus on effects of residence time and invasion status within phylogenetically-related species of the same life form (annuals) and habitat (open vegetation, ruderal and segetal habitats). We chose Asteraceae because they are one of the largest plant families globally and highly represented in plant invasions. We chose annual species because this enabled us to not only measure plant performance in terms of biomass, as usually done in competition experiments, but also total seed production, which serves as the best proxy for individual fitness, given that annuals are typically monocarpic. Minimum residence time (MRT), which is used as a proxy for the date of first introduction of a species to a new area, was extracted from various databases (Sheppard and Schurr 2019). Usually, we used seed material collected from a previous experiment conducted at the same location in 2016, where individuals had been growing in low density monoculture mesocosms (Brendel et al. 2021). Thus, we minimised potential performance differences arising from maternal effects. If this seed material was not available, we used the original seed material collected in 2015, whereby five species had been collected from wild populations in Baden-Württemberg and one species originated from a botanic garden (see Suppl. material 1: Table S1, for further details).

Target-neighbour competition experiment

In March 2017, we set up a pairwise competition experiment at a field station of the University of Hohenheim, Germany (Versuchsstation Heidfeldhof: 48°43'02.1"N, 9°11'03.1"E, 400 m a.s.l.; annual precipitation: 698 mm, mean annual temperature: 8.8 °C). The experiment was set up in a target-neighbour design, whereby we focused on five native Asteraceae as target species (*Crepis pulchra*, *Hypochaeris glabra*, *Lapsana communis*, *Pulicaria vulgaris* and *Senecio viscosus*) and all 47 species as neighbours. The five targets were grown in pots as single individuals, in intraspecific competition and in interspecific competition with all other 46 Asteraceae species, which vary in their MRT and invasion status in Germany. Thereby, we had a single target individual in the middle of the pot, surrounded by multiple individuals of one neighbour species.

The pots were placed in ten rows and each target-neighbour combination was usually replicated four times (for the total number of replicates per species combination, see Suppl. material 1: Table S1). Target-neighbour pots were set up in a fully randomised design. In total, we initially established 904 pots, of which the 20 pots with single targets and the 20 pots with intraspecific competition amongst targets, as well as 804 out of the

864 pots in the target-neighbour design had surviving individuals of both species per pot at harvest. The pots had a volume of 15-litre (0.08 m^2 soil surface area, 33 cm upper diameter, 26 cm lower diameter, 24.5 cm height) and were filled with local field soil. Prior to filling the pots, we added a layer of expanding clay to improve drainage. The pots were constantly watered throughout the growing season with an automatic drip-irrigation system and received a maximum of 1.1 litres per day during the warmest period of the year. We weeded the pots before sowing and regularly throughout the experiment.

Targets and neighbours were established from seeds. As we included such a large number of neighbour species that vary in their growth rates, we aimed for constant strength (in terms of biomass production, rather than number of individuals) of neighbour competition across species. We determined the required number of seeds to be sown for each neighbour species, based on data on the average biomass production and establishment rates from a previous experiment in 2016 (Brendel et al. 2021, see Suppl. material 1: Appendix 1, for further details). In mid-May, 3–5 seeds of the target species were added to the centre of each pot to establish the target individuals. At the same time, the species-specific amount of seeds for the neighbour species was sown around the pot centre. All seeds were covered with a thin layer of sand. We also established additional germination trays in the greenhouse to grow seedlings of the target species as back-up for transplanting (see Suppl. material 1: Appendix 1, for further details).

After setting up the target-neighbour combinations, we noticed that the pots were filled with two different soil types (which was not part of the planned design of the experiment): the field soil originated from two separate deliveries from the same company (Glaser Recycling GmbH, Mönsheim, Germany) and soil analyses indicated that these two deliveries were comparable in soil texture, but differed in nutrient contents. Specifically, we had a nutrient-poor (NO_3^- 5.48 mg/kg, NH_4^+ 0.27 mg/kg, P 3.06 mg/ kg, with a pH value of 8 and total carbon content 1.58%) and a nutrient-rich (NO_3^- 10.19 mg/kg, NH_4^+ 0.89 mg/kg, P 4.28 mg/kg, with a pH value of 7.7 and total carbon content 2.85%) soil. The soils had a sandy loamy texture (nutrient-poor type: 76% sand, 10% clay and 14% silt; nutrient-rich type: 66% sand, 16% clay and 18% silt). As having two different soil types was not a planned part of the experiment and pots had been allocated in a completely randomised manner, the target-neighbour combinations were spread unevenly between the two soil types: of the surviving pots, most pots were of the nutrient-poor type (647 pots, 16 of which are single targets), with only 21% (177 pots, four of which are single targets) in the nutrient-rich type. One species, *Carthamus tinctorius*, only occurred in the nutrient-rich soil. Having twice the amount of plant available nitrogen highly influenced biomass production during the season and, hence, we usually analysed data originating from the two soil types separately.

Four weeks after sowing, we assessed the germination success of target and neighbour species. In pots where both the target and neighbour species germinated, we thinned out the target species to one single individual. If the target did not germinate, we transplanted a target species individual from the germination trays. If the neighbour did not germinate, we re-sowed the neighbour species. Pots, in which target and neighbour still did not establish following these measures, were removed from the experiment (see Suppl. material 1: Appendix 1).

Data collection

To measure performance of targets and neighbours, we harvested aboveground biomass by mid-October 2017 (at least 17 weeks after sowing) and dried it at 70 °C for 72 hours before weighing. For the neighbours, we also counted the number of established individuals and the total number of flower heads (capitula) per pot as a proxy for reproductive output. For target individuals, reproductive output was measured more precisely, using the total seed mass produced per individual in each pot. The experimental period was long enough to allow seed production of all target species, whereby approximately two thirds of all target individuals produced seeds. To measure seed production, we collected seeds during the experiment from ideally ten intact capitula of each target individual, from which we determined the average seed mass per capitulum. Before harvesting each target individual at the end of the experiment, we counted the number of its vital capitula, to then calculate the total seed mass produced.

In addition to the experimental data, we collected data on range sizes in Germany for each species. We obtained these data from the database of FlorKart, BfN and NetPhyD Netzwerk Phytodiversität Deutschlands e.V. (www.deutschlandflora.de). This database records species occurrence in each of four quadrants of a grid cell of 10 × 6 arc minutes. We counted the number of occupied quadrants per grid cell for each species. The proportion of occupied cells for each species represents its range size in Germany (Sheppard and Schurr 2019).

Data analysis

We analysed all data in R v.4.0 (R Core Team 2020). To address the first question of whether performance in intraspecific competition depends on invasion status, we only focused on neighbour performance, assuming that the single target individual had no relevant competitive effect on its many neighbours. Except in the analysis of establishment success, to ensure this assumption was justified, we excluded all pots where target biomass was larger than neighbour biomass. This occurred in 76 out of 527 cases in the nutrient-poor and in 13 out of 156 in the nutrient-rich soil. We included all pots with surviving neighbours, which were not re-sown a second time. This resulted in 43 species for establishment and 41 species for biomass and number of capitula per pot. We were interested in pot-level performance of neighbours as a better measure for overall invasion success. For this first question of addressing intraspecific performance of neighbour species, we analysed the data of both soil types combined, but included soil type as an explanatory variable. We analysed establishment rates (the number of successfully established neighbour individuals by the end of the experiment compared to number of seeds sown) by means of a generalised linear mixed model with binomial distribution. Square-root-transformed aboveground biomass per pot and (log+1)-transformed total number of capitula per pot were analysed with a linear mixed effects model. Fixed effects included the categorical variables invasion status (a factor with four levels: casual neophyte, established neophyte, archaeophyte or native), soil type (a factor with two levels: nutrient-poor and nutrient-rich) and their interaction. Species

was included as a random effect in all models. As the number of seeds sown and seed mass differed between species, we included the log-transformed total seed mass sown per pot as a covariate in all analyses. This covariate should account for initial differences in propagule pressure, as well as potentially higher establishment success for larger seeds and density-dependent thinning for higher seed numbers. We tested significance of the explanatory variables by means of likelihood ratio tests.

For the following questions, we conducted all analyses separately for the two different soil types, because biomass production greatly differed between soil types (see "Competition pressure"). Some of the analyses could only be done for the pots with nutrient-poor soil, for which we had considerably more replicates (see Suppl. material 1: Table S1, for species-specific sample sizes). To address the second question of whether competitive response of targets or competitive effects of neighbours depend on residence time or invasion status, we used two approaches. First, to explore the native targets' tolerance to competition (competitive response), we used a linear mixed effects model to investigate the effect of neighbour biomass on target aboveground biomass and total seed mass, depending on either MRT or invasion status and their interaction with neighbour biomass. Given that the native targets have the longest MRTs, the neighbour MRT here represents the length of potential co-existence times between native targets and neighbours. Aboveground target and neighbour biomass was square-root-transformed in all analyses to meet model assumptions, while the total seed mass was (log+0.001)- and MRT log-transformed. Given that seed production was possible (the individuals survived and all target species produced seeds at least in some instances), we included the zero values in this analysis. We included random effects of target and neighbour species identity. Models using the explanatory variable MRT versus invasion status were compared via the Akaike Information Criterion (AIC), while the significance of the interaction between MRT (or invasion status, respectively) and neighbour biomass was tested with likelihood ratio tests. To ensure that effects are not due to targets being differently affected by transplanting or re-sowing, we conducted a control analysis excluding all pots with transplanted target individuals and/or re-sown neighbours.

Second, we estimated the competitive effect of each neighbour species on the targets. For each neighbour species separately, square-root-transformed neighbour biomass was regressed against square-root-transformed target biomass (across all five target species), including all data from interspecific competition in the nutrient-poor soil (for species-specific sample sizes, see Suppl. material 1: Table S2). The slope of this regression represents the strength of the competitive effect. We then tested in a linear model if the competitive effect of the 46 neighbour species (*C. tinctorius* had to be excluded as it only occurred in nutrient-rich soil) was related to log-transformed MRT or invasion status, again comparing the two models via AIC. To account for the fact that the species-specific regressions varied in their sample sizes and goodness of fit, we weighted the regressions by the inverse of the squared standard error of the slope. However, to highlight the effect of weighing, we below also show the results of non-weighted regression. Due to a lack of data points, competitive effects were not estimated for the nutrient-rich soil type.

To address the third research question of whether interspecific competitive effects influence range size when accounting for MRT, we assessed in another weighted regression model whether per-capita competitive effects influence range size. Range size was defined as the logit-transformed proportion of area occupied in Germany and we included log-transformed MRT as a covariate. Per-capita competitive effects were again derived from the slope of the species-specific regressions described above and we used the inverse of the squared standard error of the slope as weights.

Data resources

The data underpinning the analysis reported in this paper are deposited in the Dryad Data Repository at https://doi.org/10.5061/dryad.qrfj6q5ff.

Results

Competition pressure

The number of neighbour individuals in the nutrient-poor soil type ranged between 1 and 22 (median 4, mean 5.1), except for the casual neophyte *Callistephus chinensis*, which reached up to 53 individuals. Nevertheless, this species was within the range of neighbour biomass covered by other species: neighbour biomass ranged from 0.01–15.6 g (median 4.0 g, mean 4.7 g). In the nutrient-rich soil type, between 1 and 33 (for *C. chinensis*, up to 42) neighbour individuals established (median 5, mean 6.0). Neighbour biomass in the nutrient-rich soil ranged from 0.21–68.3 g (median 16.2, mean 19.5 g). Target species were usually negatively affected by competition, whereby their biomass production greatly varied depending on neighbour species (see Suppl. material 1: Fig. S2).

Performance in intraspecific competition

Establishment success was not affected by the interaction between soil type and invasion status ($\chi^2_{3df} = 4.44$, $P = 0.218$), with the full model only explaining 9.9% (marginal R^2; 85.7% with random effects, i.e. conditional R^2) of variance in the data (Fig. 1a). We then tested for significance of the main effects in a reduced model without the interaction. Neither the main effects of soil type ($\chi^2_{1df} = 0.88$, $P = 0.349$) nor invasion status ($\chi^2_{3df} = 5.03$, $P = 0.170$) were significant, nor even the covariate total seed mass sown.

However, the interaction between soil type and invasion status was highly significant for aboveground biomass (Fig. 1b; $\chi^2_{3df} = 64.5$, $P < 0.001$), with the model explaining 74.1% (87.5% with random effects) of the variance. In separate models for the two soil types, differences in invasion status were highly significant (nutrient-poor soil type: $\chi^2_{3df} = 31.83$, $P < 0.001$, with marginal R^2 of 45.4% and conditional R^2 of 72.7%; nutrient-rich soil type: $\chi^2_{3df} = 21.43$, $P < 0.001$, with marginal R^2 of 38.3% and conditional R^2 of 69.1%). While biomass was generally considerably higher in the nutrient-rich soil, in both soil types, casual neophytes produced most biomass and na-

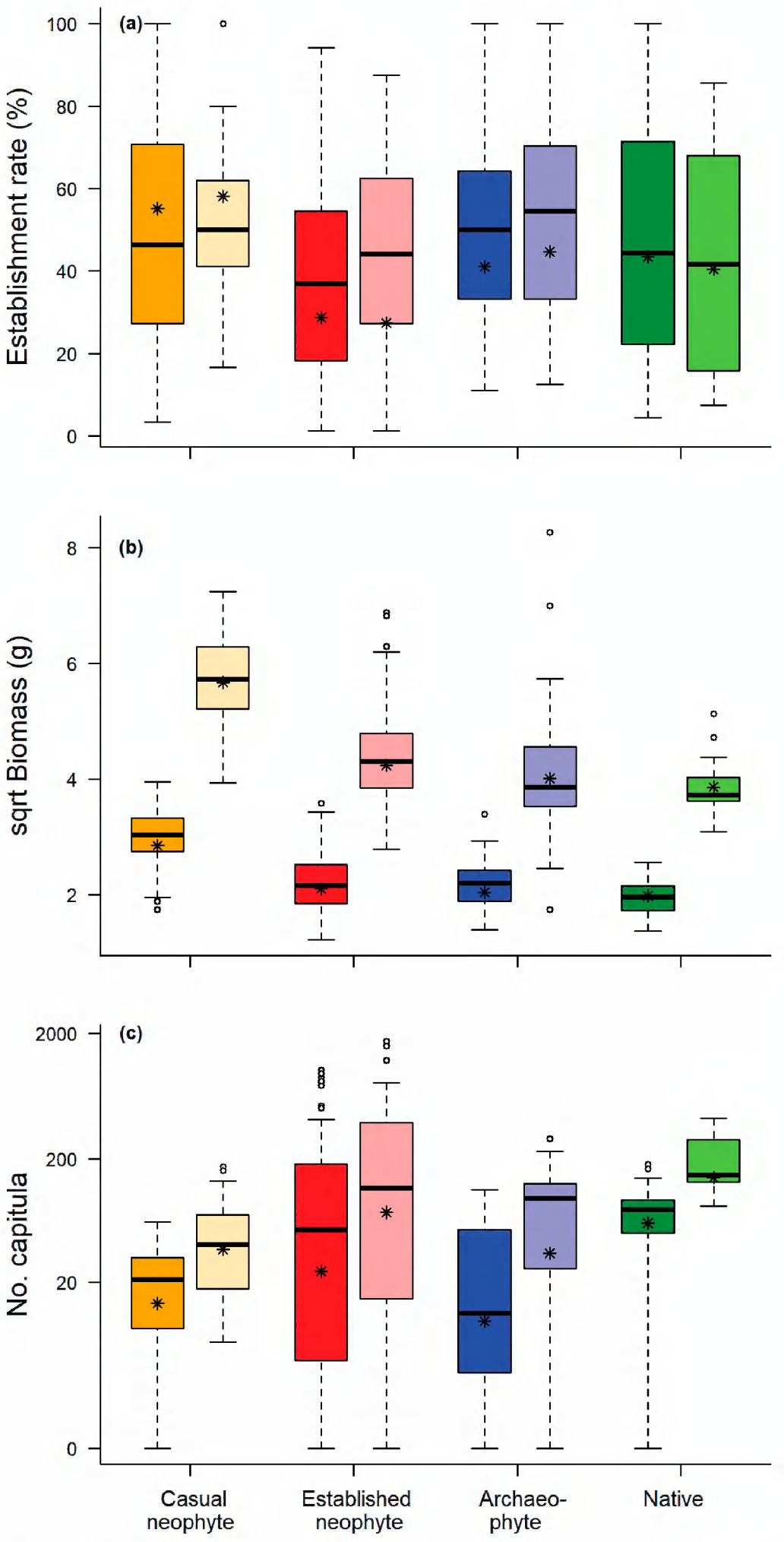

Figure 1. Performance in intraspecific competition at pot-level depending on invasion status and soil type (left bars in darker colours show the nutrient-poor and right bars in lighter colour the nutrient-rich soil type). Performance is shown as **a** establishment success (n = 527/156 in the nutrient-poor/nutrient-rich soil type) **b** square-root-transformed aboveground biomass per pot (n = 451/143) and **c** total number of capitula per pot (shown on a log-scale, n = 449/143). The asterisks show the mean performance per invasion status group and soil type.

tives the least and this difference was more pronounced in nutrient-rich soil (Fig. 1b). Note that these results remained qualitatively similar when removing *C. chinensis* from the analysis, given that this was the casual neophyte that established in considerably higher number of individuals than other species.

For number of capitula, the interaction between soil type and invasion status was not significant (Fig. 1c; $\chi^2_{3df} = 6.15$, $P = 0.104$). The model explained 18.1% (90.2% with random effects) of variance in the data. Testing for significance of the main effects in a reduced model without the interaction showed that more capitula were produced in the nutrient-rich soil ($\chi^2_{1df} = 266.49$, $P < 0.001$), while the effect of invasion status was not significant ($\chi^2_{3df} = 5.99$, $P = 0.112$), although the data suggest that established neophytes and natives tended to produce more capitula compared to casual neophytes and archaeophytes.

Competitive response and competitive effects

The models testing the effect of invasion status instead of minimum residence time (MRT) on competitive responses resulted in lower AIC and thus better model performance for both aboveground biomass and total seed mass of native targets in the nutrient-poor soil (Table 1). Thereby, we did not find directional changes in competitive ability in respect to target biomass (i.e. only a marginally significant interaction between MRT and neighbour biomass, Fig. 2a). Instead, we found a significant interaction between neighbour biomass and invasion status (Fig. 2b): native targets generally showed lowest tolerance to competition from natives and established neophytes and were least affected by competition from casual neophytes. For target seed mass, the direction of effects was the same as for biomass (Fig. 2c, d), but the interactions were not significant (Table 1). The control analysis without transplanted targets or re-sown neighbours resulted in qualitatively similar effects (see Suppl. material 1: Fig. S3). In the nutrient-rich soil (Fig. 3), for total seed mass of targets, the model with MRT re-

Table 1. Models analysing effects of neighbour biomass on target performance depending on minimum residence time (MRT) or invasion status. For each target performance measure (aboveground biomass and total seed mass, sample sizes for the nutrient-poor and nutrient-rich soil type in parentheses), differences in the Akaike Information Criterion (ΔAIC), explained variance (marginal R^2 and, in parentheses, conditional R^2) and results of likelihood ratio tests (LRT, χ^2 with degrees of freedom and *P*-values) for the interaction between MRT and neighbour biomass or invasion status and neighbour biomass, are shown. Analyses were done separately for the nutrient-poor and nutrient-rich soil type.

Model	Soil type	Target biomass (n = 615/168)			Target total seed mass (n = 607/167)		
		ΔAIC	R-squared	LRT	ΔAIC	R-squared	LRT
MRT	Nutrient-poor	6.12	58.4 (71.6)	$\chi^2_{1df} = 3.34$, $P = 0.067$	2.75	13.3 (55.6)	$\chi^2_{1df} = 0.98$, $P = 0.322$
Invasion status	Nutrient-poor	0	59.6 (72.4)	($\chi^2_{3df} = 15.67$, $P = 0.001$	0	14.9 (56.0)	$\chi^2_{3df} = 5.62$, $P = 0.132$
MRT	Nutrient-rich	3.20	47.7 (68.4)	$\chi^2_{1df} = 3.33$, $P = 0.068$	0	19.1 (47.3)	$\chi^2_{1df} = 2.07$, $P = 0.150$
Invasion status	Nutrient-rich	0	49.6 (72.3)	$\chi^2_{3df} = 13.04$, $P = 0.005$	1.07	22.6 (49.6)	$\chi^2_{3df} = 7.24$, $P = 0.065$

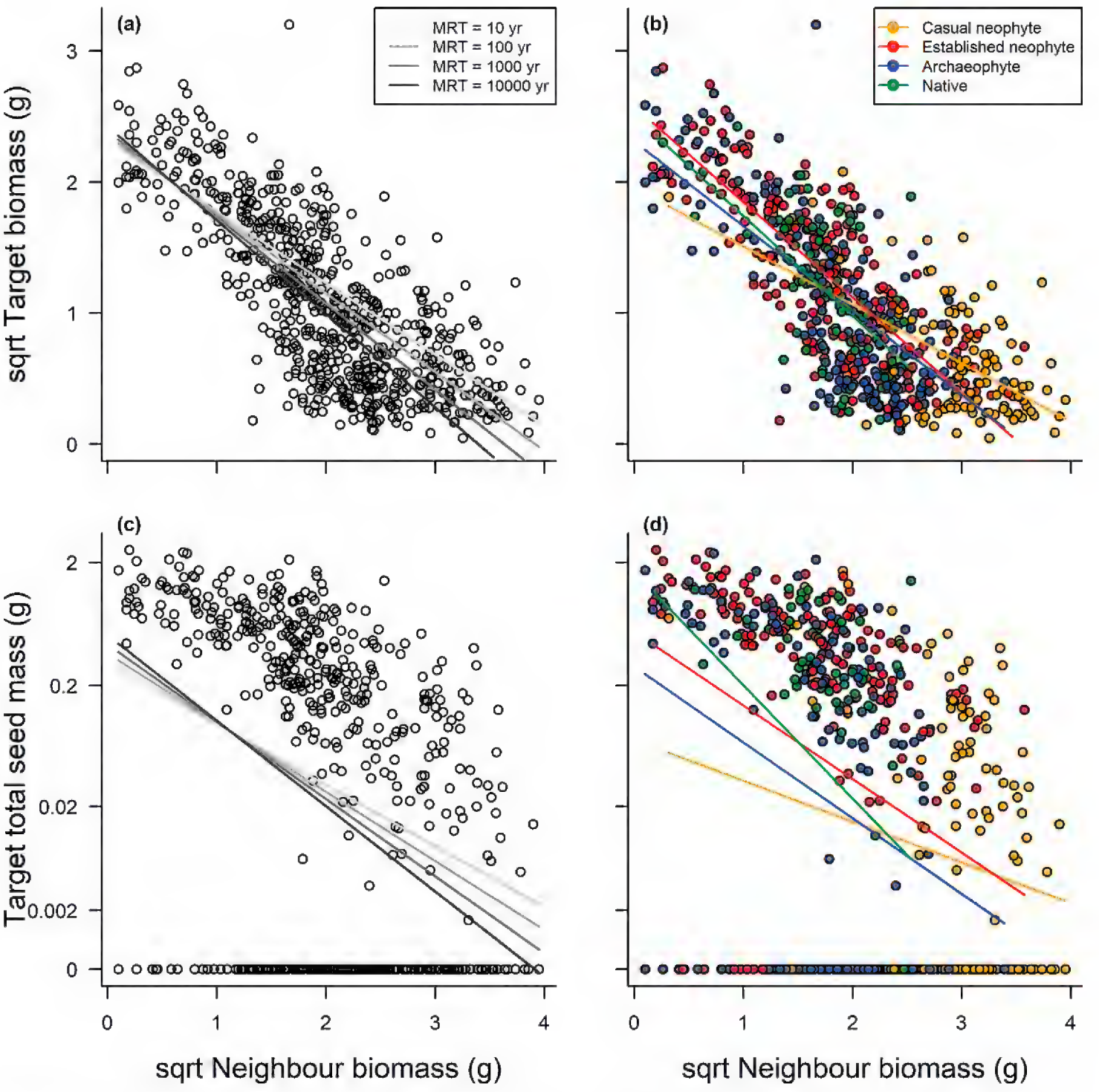

Figure 2. Effects of square-root-transformed neighbour biomass on target performance **a, b** square-root-transformed aboveground biomass (n = 615) and **c, d** total seed mass (shown on a log-scale, n = 607), depending on **a, c** minimum residence time (MRT) or **b, d** invasion status in the nutrient-poor soil. To illustrate the interaction between continuous MRT and neighbour biomass in (**a, c**), a few representative values were chosen.

sulted in lower AIC (Table 1). This model predicted higher tolerance of native targets to competition from neighbour species with higher MRT (in line with the hypothesis of increasing biotic resistance over time, Fig. 3c, although note that the interaction between MRT and neighbour biomass was not significant). Conversely, predictions for the invasion status models were similar to the nutrient-poor soil (Fig. 3b, d).

The regression models to determine competitive effects of the 46 species ranged in R^2 from 0.5–87.7% (mean 41.6%, median 41.9%), with 33 species having *P*-values lower than 0.05 (see Suppl. material 1: Table S2). MRT had a negative effect on the slope (competitive effect) of these species-specific regressions ($F_{1,44}$ = 8.20,

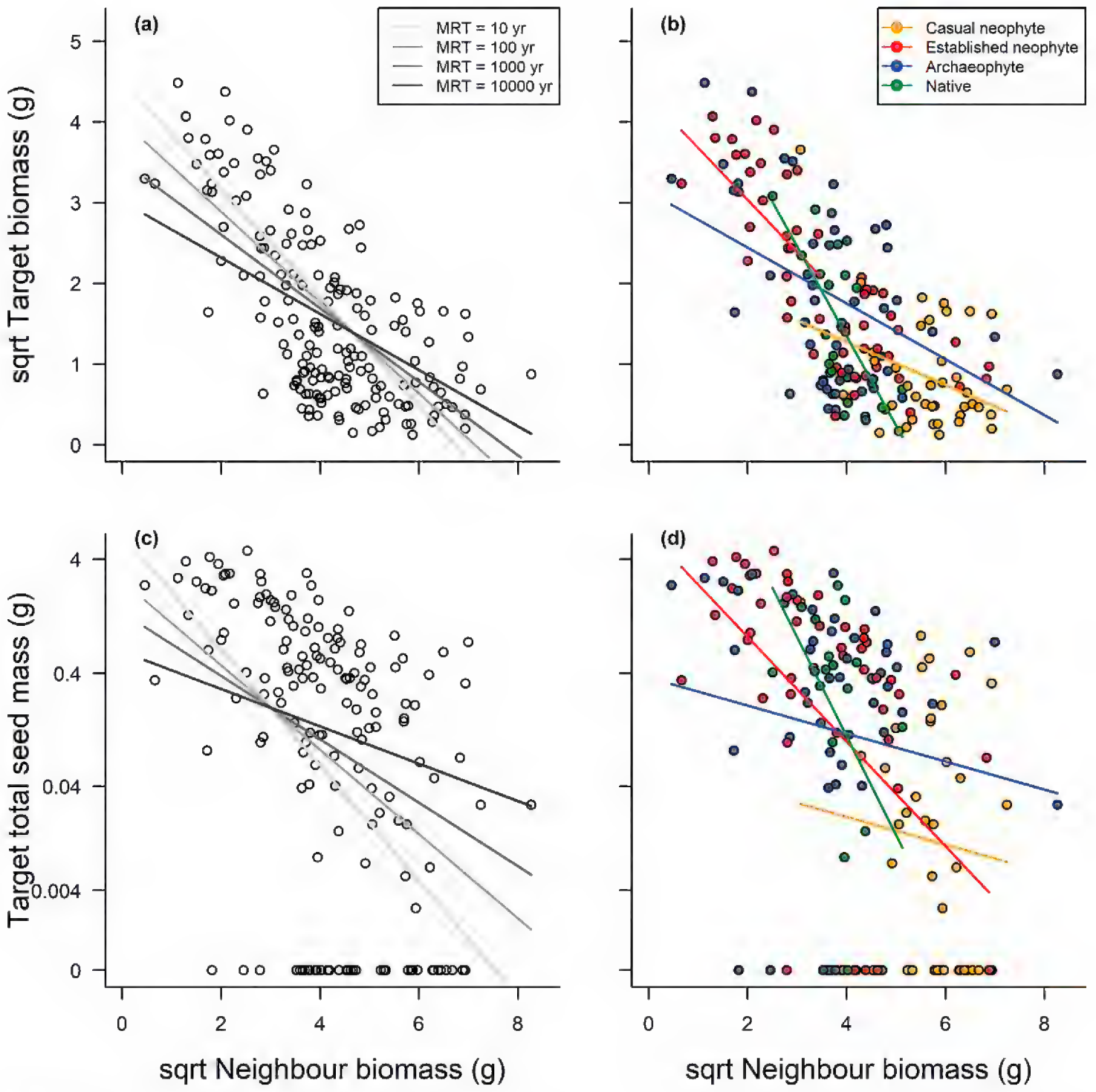

Figure 3. Effects of square-root-transformed neighbour biomass on target performance **a, b** square-root-transformed aboveground biomass (n = 168) and **c, d** total seed mass (shown on a log-scale, n = 167), depending on **a, c** minimum residence time (MRT) or **b, d** invasion status in the nutrient-rich soil. To illustrate the interaction between continuous MRT and neighbour biomass in (**a, c**), a few representative values were chosen.

$P = 0.006$), explaining 15.7% of variance in the data (whereas, if using non-weighted regression, effect size was weaker and not significant). Hence, species with longer residence times have larger competitive effects (Fig. 4a). However, the invasion status model was better with a difference in AIC (ΔAIC) of 12.05, showing a highly significant effect of invasion status ($F_{3,42} = 9.54$, $P < 0.001$, Fig. 4b) and explaining 40.5% of variance in the data (however, without weighting, only half the variance was explained for the invasion status model which was still better by ΔAIC = 3.72). Casual neophytes had the weakest, established neophytes and natives the strongest competitive effects (Fig. 4b).

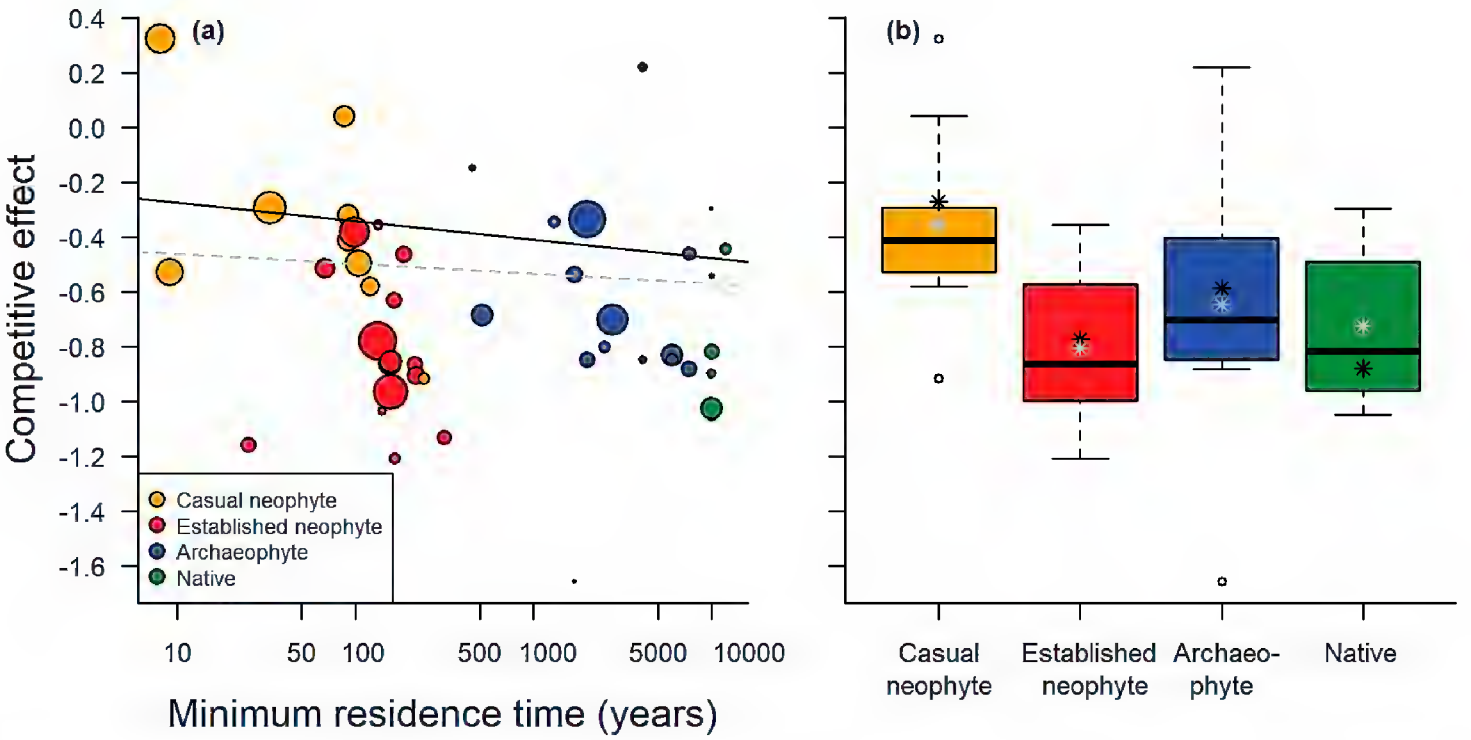

Figure 4. Effects of **a** minimum residence time or **b** invasion status on the competitive effect (slope of species-specific regressions). In **a** size of circles shows the square root of the inverse of the standard error of the slope to illustrate weights of data points. The grey dashed line shows the regression line without weighting for comparison. In **b** the asterisks show the mean competitive effect per invasion status group (in black, in grey for the model without weighting).

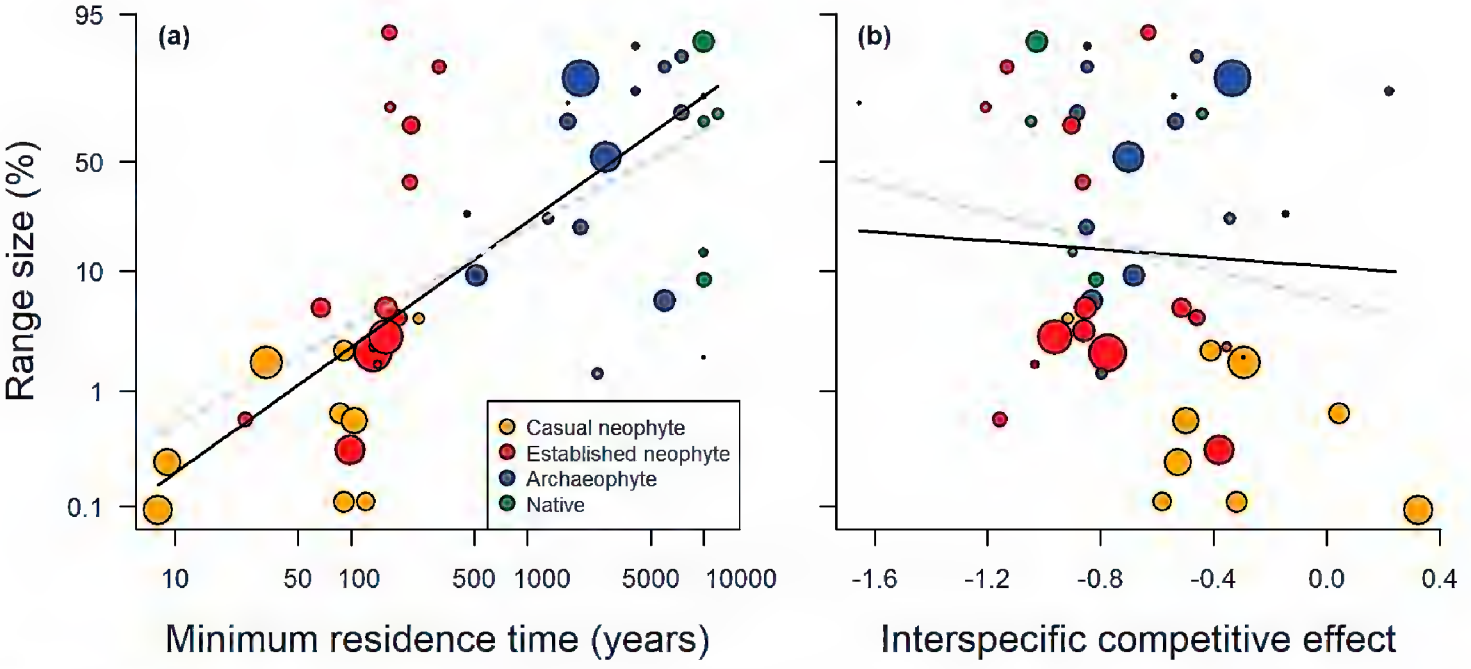

Figure 5. Effects of **a** minimum residence time (MRT) and **b** interspecific competitive effect (slope of species-specific regressions) on range size in Germany (model predictions shown with the other explanatory variable fixed at its mean). Size of circles show **a, b** the square root of the inverse of the standard error of the slope to illustrate weights of data points. The grey dashed lines show regression lines without weighting for comparison.

Competitive effect and range size

When controlling for the highly significant positive effect of MRT on range size ($F_{1,43}$ = 69.33, P < 0.001, Fig. 5a), the slope (per-capita interspecific competitive effect,

whereby lower values indicate stronger effects) of the species-specific regressions did not significantly affect range sizes in Germany ($F_{1,43} = 0.25$, $P = 0.618$, Fig. 5b; although, without weighting, there was a marginally significant negative effect, meaning that more competitive species tended to have larger range sizes). The model explained 61.8% of variance in range sizes.

Discussion

Competitive ability in relation to residence time: is there evidence for directional eco-evolutionary changes in competitive ability?

Our results showed that interspecific competitive ability was generally better explained by categorical invasion status compared to continuous residence time. However, total seed production of targets tended to be less affected by competition with neighbours the longer their potential co-existence times in the nutrient-rich soil. This pattern is consistent with the hypothesis of increasing eco-evolutionary experience (Saul et al. 2013) of targets leading to higher biotic resistance to newly-introduced species over time. Thereby, total seed production greatly varied in our experiment from no seeds at all to a large reproductive output. Given that seed production serves as the best measure of individual fitness for annual species, this variation in response to competition should thus have direct consequences on native population growth and persistence.

Invasions provide a natural experiment with which we can test if plant-plant interactions can drive evolution (Thorpe et al. 2011). Provided that competition is important for fitness and that there is genetic variation in traits related to competitive ability, we may expect adaptation to new competitors over time as a result of natural selection (Lankau 2011). From the perspective of a native plant community (consisting of perennial ruderal grassland species, no Asteraceae), rather than pairwise interactions, Sheppard and Schurr (2019) previously found evidence of increasing biotic resistance to invasion by Asteraceae species of increasing residence times. There are several explanations why, in this study, we only found limited evidence of such an effect. First, context-dependence is clearly important, as highlighted by the contrasting results from the two soil types. Other studies have also found that, in contrast to the competitive effect, competitive response was not consistent with nutrient levels or neighbour identity (Wang et al. 2010). Second, eco-evolutionary changes in competitive ability may simply not be relevant enough in contrast to *a priori* differences: even under strong selective forces, there are factors constraining adaptation, such as plasticity, spatial heterogeneity in selective forces, gene flow, lack of additive genetic variance, negative genetic correlations or unfavourable demography and population structure (Strauss et al. 2006; Thorpe et al. 2011). Third, instead of, or additionally to, adaptive responses of native plant species to novel competitive interactions, other eco-evolutionary changes in biotic interactions may decrease (or increase) invader performance over time (e.g. Lankau et al. 2009; Dostál et al. 2013; Gruntman et al. 2017; Aldorfová et al. 2020), potentially confounding effects. Finally, there are some limitations with our multi-spe-

cies approach, because not all study species are necessarily bound to co-occur, meaning that the neighbour's residence time is only a proxy for length of co-existence time with the native target. To minimise this issue, we used a large set of study species, so that individual species pairs should have limited effects on the results and selected species from the same habitats and sourced them in the same region as far as was possible. Nevertheless, even when finding a pattern consistent with our hypothesis. such as in the nutrient-rich soil, we cannot prove that it results from evolutionary adaptation over time. For this, we would need to experimentally manipulate the presence of alien species and compare performance of naïve and experienced native genotypes (Strauss et al. 2006), which considerably limits the temporal scale that can be studied. Hence, to better understand changes in competitive interactions with increasing length of co-existence time, our approach should be combined with studies on population differences within a species (e.g. Germain et al. 2020), whereby to provide conclusive evidence, experiments ideally would be coupled with genetic analyses.

Differences in performance and competitive ability depending on invasion status

The finding that invasion status mostly better explained differences in competitive ability compared to residence time might be because of *a priori* differences between species types due to an introduction bias. Although invasion status can also serve as a proxy for residence time, our results do not support increasing biotic resistance by native species to newly-introduced species as a mechanism, because we did not find directional effects: archaeophytes generally ranked intermediate, with both natives and established neophytes performing best, whereby native targets showed the lowest tolerance to competition from these two groups. Besides introduction bias, these differences might arise from other eco-evolutionary processes that are more specific to certain invasion status groups (e.g. evolution of increased competitive ability hypothesis, Blossey and Nötzold 1995). However, we here did not find support for the often invoked hypothesis that established alien species have higher competitive ability than natives, which may have several reasons. Recent meta-analyses on pairwise plant interactions between natives and aliens found such higher competitive ability only in particular cases which we did not test here: invasive alien species had greater competitive effects on native species than on non-invasive alien species (Kuebbing and Nuñez 2016) and alien plants were better response competitors than native plants (whereas in line with our results, they did not have larger competitive effects than natives, Golivets and Wallin 2018). In addition, as previously suggested, whether aliens and natives differ may also depend on the types of alien and native species comparisons are made (Vilà and Weiner 2004). For instance, in a multi-species experiment, Zhang and van Kleunen (2019) quantified competitive outcomes between 48 pairs of 17 annual natives and established alien neophytes. They found that common aliens (defined as species that are widespread and locally abundant, only two categories: common or rare) were not more competitive than common natives, but only than rare natives.

Furthermore, that aliens themselves are not a uniform category is shown by the substantial differences between casual and established aliens in our study, which may also have important management implications.

Most studies to date did not consider casual neophytes. Indeed, Kuebbing and Nuñez (2016) hypothesised that interaction patterns including casuals may likely differ from established or invasive aliens, but they did not include casuals in their meta-analysis due to the lack of studies available. Casual aliens, as a category, may be more variable in performance than other groups since they have only passed through the transport and introduction stage of the invasion, but not yet through subsequent filters determining establishment and spread (Blackburn et al. 2011). This group includes species that are casual because they did not have enough time to establish, which is indicated by the generally lower residence times (see Suppl. material 1: Fig. S1) and are described by the concept of lag phases (Aikio et al. 2010) or invasion debt (Rouget et al. 2016). This group, however, also includes species that are not successful enough to establish and hence will disappear again with time, representing failed invasions. Thus, it may not be surprising that this group was found to have the weakest per-capita interspecific competitive effects. One species, *Bidens ferulifolia*, may even facilitate other species, a finding and potential mechanisms that should be further investigated in future studies. The finding that casual neophytes, as a group, produced the highest biomass in intraspecific competition may be because weak competitors generally tolerate intraspecific competition better than interspecific competition (Stoll and Prati 2001). The high biomass production of casual aliens in intraspecific competition also did not lead to higher reproductive output, which could explain why casual neophytes were not yet able to establish self-sustaining populations, even when establishment success did not differ amongst invasion status groups. However, we note that, due to our experimental design that aimed for similar competition pressures amongst species in terms of aboveground biomass production, achieved population densities differed between species due to differing number of seeds sown and additionally differed between replicates due to varying establishment success. Although we corrected for these differences in propagule pressure in our analysis, density-dependence may limit inference of our results. Additionally, since we did not have a true intraspecific competition treatment for the majority of species, the target species may still have had an effect on its neighbours.

Finally, the archaeophytes had the weakest competitive effects after the casual neophytes and an intermediate rank in terms of the native species tolerance to these neighbours. Archaeophytes generally occur in similar habitats to neophytes, but have quite different introduction histories (Chytrý et al. 2008). Their weaker competitive ability may also explain, to some extent, why some archaeophytes are threatened nowadays due to the intensifications in land use. Although they are alien species, their threatened status may be unfortunate, since, as segetal weeds, they are valued for their function in increasing biodiversity in agricultural landscapes (Zając et al. 2009).

Scaling up: relationships between competitive effect and range size

Invasion success may also result from other mechanisms than interspecific competitive superiority. According to the Parker equation, the impact of an invader is the product of abundance, per-capita competitive effects and range sizes (Parker et al. 1999). As several studies have shown before for alien species, residence time strongly influenced range sizes (Pyšek and Jarošík 2005; Williamson et al. 2009; Pyšek et al. 2015). When testing whether large-scale success is associated with local success, we found that per-capita interspecific competitive effects did not influence range sizes. Although a couple of studies previously found that more competitive alien species reach larger range sizes (Milla et al. 2011; Sheppard 2019), there are numerous explanations why this might not be the case. Particularly for species with limited residence time, range sizes may depend more on dispersal ability or human introductions. Furthermore, range sizes may also be influenced by herbivory or pollinators (Svenning et al. 2014). We consider it unlikely that variation in the size of potentially suitable habitat may mask effects, as the choice of species was based on similar habitat preference, whereby ruderal and segetal habitats are widespread across Germany. Furthermore, although the species originate from different parts of the world, the species' potentially suitable habitat in Germany, based on climatic niches, is high according to estimates from a previous study (i.e. larger than 90%, calculated using Mahalanobis distances, including all focal species, except four, Sheppard and Schurr 2019).

However, a study on the whole German flora showed that the traits that influence range sizes differed amongst neophytes, archaeophytes and natives (Knapp and Kühn 2012), in which case we may not expect to find a consistent effect across the whole alien-native species continuum considered here. Furthermore, the lack of association between competitive ability and range size may also indicate that our species are r-selected, with fast growth and with it spread in non-competitive environments (Dietz and Edwards 2006). This is a strategy frequently observed in annual species of ruderal habitats, such as we studied here. In fact, for an almost identical set of study species, we previously found evidence for intra- or interspecific selection towards ruderality with increasing residence time: annual Asteraceae species with lower seed mass had higher finite rates of increase and, consistent with selection, species with long residence times had low seed mass (Brendel et al. 2021).

Conclusions

Using an alien-native species continuum to investigate pairwise competition amongst 47 Asteraceae species, in this study, we found little evidence of directional changes in competitive ability over long timescales. Large-scale invasion success was also not explained by small-scale competitive ability. Further, despite the well justified reasons to argue that human-mediated invasions differ from natural colonisation (Wilson et al. 2016), we here did not find differences specifically between established neophytes and natives in terms of intra- and interspecific competitive

ability. However, there may be other *a priori* differences resulting from an introduction bias and other mechanisms resulting from different eco-evolutionary processes by which the aliens can utilise their novelty to impact on natives that we did not consider here. Further studies across a broader range of environmental conditions, involving other biotic interactions that may indirectly influence plant-plant interactions, may shed light on the contexts in which eco-evolutionary adaptations to new invaders are a relevant mechanism.

Acknowledgements

This research was financially supported by the German Research Foundation (grant SH 924/1-1). We are grateful to C. Buchmann, B. Springer, S. Hansen, H. Oliphant and interns from the IAESTE programme for their assistance with the competition experiment.

References

Aikio S, Duncan RP, Hulme PE (2010) Lag-phases in alien plant invasions: separating the facts from the artefacts. Oikos 119: 370–378. https://doi.org/10.1111/j.1600-0706.2009.17963.x

Aldorfová A, Knobová P, Münzbergová Z (2020) Plant–soil feedback contributes to predicting plant invasiveness of 68 alien plant species differing in invasive status. Oikos 129: 1257–1270. https://doi.org/10.1111/oik.07186

Blackburn TM, Pyšek P, Bacher S, Carlton JT, Duncan RP, Jarošík V, Wilson JRU, Richardson DM (2011) A proposed unified framework for biological invasions. Trends in Ecology and Evolution 26: 333–339. https://doi.org/10.1016/j.tree.2011.03.023

Blossey B, Nötzold R (1995) Evolution of increased competitive ability in invasive nonindigenous plants – a hypothesis. Journal of Ecology 83: 887–889. https://doi.org/10.2307/2261425

Brendel MR, Schurr FM, Sheppard CS (2021) Inter- and intraspecific selection in alien plants: how population growth, functional traits and climate responses change with residence time. – Global Ecology and Biogeography 30: 429–442. https://doi.org/10.1111/geb.13228

Buckley YM, Catford J (2016) Does the biogeographic origin of species matter? Ecological effects of native and non-native species and the use of origin to guide management. Journal of Ecology 104: 4–17. https://doi.org/10.1111/1365-2745.12501

Bytheway JP, Banks PB (2019) Overcoming prey naiveté: Free-living marsupials develop recognition and effective behavioral responses to alien predators in Australia. Global Change Biology 25: 1685–1695. https://doi.org/10.1111/gcb.14607

Callaway RM, Aschehoug ET (2000) Invasive plants versus their new and old neighbors: a mechanism for exotic invasion. Science 290: 521–523. https://doi.org/10.1126/science.290.5491.521

Callaway RM, Ridenour WM, Laboski T, Weir T, Vivanco JM (2005) Natural selection for resistance to the allelopathic effects of invasive plants. Journal of Ecology 93: 576–583. https://doi.org/10.1111/j.1365-2745.2005.00994.x

Chytrý M, Maskell LC, Pino J, Pyšek P, Vilà M, Font X, Smart SM (2008) Habitat invasions by alien plants: a quantitative comparison among Mediterranean, subcontinental and oceanic regions of Europe. Journal of Applied Ecology 45: 448–458. https://doi.org/10.1111/j.1365-2664.2007.01398.x

Colautti RI, Barrett SCH (2013) Rapid adaptation to climate facilitates range expansion of an invasive plant. Science 342: 364–366. https://doi.org/10.1126/science.1242121

Dietz H, Edwards PJ (2006) Recognition that causal processes change during plant invasion helps explain conflicts in evidence. Ecology 87: 1359–1367. https://doi.org/10.1890/0012-9658(2006)87[1359:RTCPCD]2.0.CO;2

Dostál P, Müllerová J, Pyšek P, Pergl J, Klinerová T (2013) The impact of an invasive plant changes over time. Ecology Letters 16: 1277–1284. https://doi.org/10.1111/ele.12166

Germain RM, Srivastava D, Angert AL (2020) Evolution of an inferior competitor increases resistance to biological invasion. Nature Ecology & Evolution 4: 419–425. https://doi.org/10.1038/s41559-020-1105-x

Golivets M, Wallin KF (2018) Neighbour tolerance, not suppression, provides competitive advantage to non-native plants. Ecology Letters 21: 745–759. https://doi.org/10.1111/ele.12934

Griggs RF (1940) The ecology of rare plants. Bulletin of the Torrey Botanical Club 67: 575–594. https://doi.org/10.2307/2481578

Gruntman M, Segev U, Glauser G, Tielbörger K (2017) Evolution of plant defences along an invasion chronosequence: defence is lost due to enemy release – but not forever. Journal of Ecology 105: 255–264. https://doi.org/10.1111/1365-2745.12660

Guo W-Y, Kleunen M van, Pierce S, Dawson W, Essl F, Kreft H, Maurel N, Pergl J, Seebens H, Weigelt P, Pyšek P (2019) Domestic gardens play a dominant role in selecting alien species with adaptive strategies that facilitate naturalization. Global Ecology and Biogeography 28: 628–639. https://doi.org/10.1111/geb.12882

Hawkes CV (2007) Are invaders moving targets? The generality and persistence of advantages in size, reproduction, and enemy release in invasive plant species with time since introduction. The American Naturalist 170: 832–843. https://doi.org/10.1086/518206

van Kleunen M, Weber E, Fischer M (2010) A meta-analysis of trait differences between invasive and non-invasive plant species. Ecology Letters 13: 235–245. https://doi.org/10.1111/j.1461-0248.2009.01418.x

van Kleunen M, Dawson W, Bossdorf O, Fischer M (2014) The more the merrier: multi-species experiments in ecology. Basic and Applied Ecology 15: 1–9. https://doi.org/10.1016/j.baae.2013.10.006

Knapp S, Kühn I (2012) Origin matters: widely distributed native and non-native species benefit from different functional traits. Ecology Letters 15: 696–703. https://doi.org/10.1111/j.1461-0248.2012.01787.x

Kuebbing SE, Nuñez MA (2016) Invasive non-native plants have a greater effect on neighbouring natives than other non-natives. Nature Plants 2: e16134. https://doi.org/10.1038/nplants.2016.134

Lambdon PW, Pyšek P, Basnou C, Hejda M, Arianoutsou M, Essl F, Jarošík V, Pergl J, Winter M, Anastasiu P, Andriopoulos P, Bazos I, Brundu G, Celesti-Grapow L, Chassot P, Delipetrou P, Josefsson M, Kark S, Klotz S, Kokkoris Y, Kühn I, Marchante H, Perglová I, Pino

J, Vilà M, Zikos A, Roy DB, Hulme PE (2008) Alien flora of Europe: Species diversity, temporal trends, geographical patterns and research needs. Preslia 80: 101–149.

Lankau RA (2011) Rapid Evolutionary Change and the Coexistence of Species. Annual Review of Ecology, Evolution, and Systematics 42: 335–354. https://doi.org/10.1146/annurev-ecolsys-102710-145100

Lankau RA (2012) Coevolution between invasive and native plants driven by chemical competition and soil biota. Proceedings of the National Academy of Sciences 109: 11240–11245. https://doi.org/10.1073/pnas.1201343109

Levine JM, Vilà M, D'Antonio CM, Dukes JS, Grigulis K, Lavorel S (2003) Mechanisms underlying the impacts of exotic plant invasions. Proceedings of the Royal Society B: Biological Sciences 270: 775–781. https://doi.org/10.1098/rspb.2003.2327

Lloyd KM, Lee WG, Wilson JB (2002) Competitive abilities of rare and common plants: comparisons using Acaena (Rosaceae) and Chionochloa (Poaceae) from New Zealand. Conservation Biology 16: 975–1985. https://doi.org/10.1046/j.1523-1739.2002.01033.x

Milla R, Iriondo AEM (2011) Congruence between geographic range distribution and local competitive ability of two Lupinus species. American Journal of Botany 98: 1456–1464. https://doi.org/10.3732/ajb.1000519

Oduor AMO (2013) Evolutionary responses of native plant species to invasive plants: a review. New Phytologist 200: 986–992. https://doi.org/10.1111/nph.12429

Ordonez A, Wright IJ, Olff H (2010) Functional differences between native and alien species: a global-scale comparison. Functional Ecology 24: 1353–1361. https://doi.org/10.1111/j.1365-2435.2010.01739.x

Parker IM, Simberloff D, Lonsdale WM, Goodell K, Wonham M, Kareiva PM, Williamson MH, Holle BV, Moyle PB, Byers JE, Goldwasser L (1999) Impact: toward a framework for understanding the ecological effects of invaders. Biological Invasions 1: 3–19. https://doi.org/10.1023/A:1010034312781

Pyšek P, Jarošík V (2005) Residence time determines the distribution of alien plants. In: Inderjit P (Ed.) Invasive Plants: Ecological and Agricultural Aspects. Birkhäuser Basel, 77–96. https://doi.org/10.1007/3-7643-7380-6_5

Pyšek P, Manceur AM, Alba C, McGregor KF, Pergl J, Štajerová K, Chytrý M, Danihelka J, Kartesz J, Klimešová J, Lučanová M, Moravcová L, Nishino M, Sádlo J, Suda J, Tichý L, Kühn I (2015) Naturalization of central European plants in North America: species traits, habitats, propagule pressure, residence time. Ecology 96: 762–774. https://doi.org/10.1890/14-1005.1

Pyšek P, Hulme PE, Simberloff D, Bacher S, Blackburn TM, Carlton JT, Dawson W, Essl F, Foxcroft LC, Genovesi P, Jeschke JM, Kühn I, Liebhold AM, Mandrak NE, Meyerson LA, Pauchard A, Pergl J, Roy HE, Seebens H, Kleunen M van, Vilà M, Wingfield MJ, Richardson DM (2020) Scientists' warning on invasive alien species. Biological Reviews 95: 1511–1534. https://doi.org/10.1111/brv.12627

R Core Team (2020) R: A language and environment for statistical computing. R Foundation for Statistical Computing, Vienna. https://www.R-project.org/

Rouget M, Robertson MP, Wilson JRU, Hui C, Essl F, Renteria JL, Richardson DM (2016) Invasion debt – quantifying future biological invasions. Diversity and Distributions 22: 445–456. https://doi.org/10.1111/ddi.12408

Saul W-C, Jeschke JM, Heger T (2013) The role of eco-evolutionary experience in invasion success. NeoBiota 17: 57–74. https://doi.org/10.3897/neobiota.17.5208

Sheppard CS (2019) Relative performance of co-occurring alien plant invaders depends on traits related to competitive ability more than niche differences. Biological Invasions 21: 1101–1114. https://doi.org/10.1007/s10530-018-1884-z

Sheppard CS, Schurr FM (2019) Biotic resistance or introduction bias? Immigrant plant performance decreases with residence times over millennia. Global Ecology and Biogeography 28: 222–237. https://doi.org/10.1111/geb.12844

Simberloff D, Martin JL, Genovesi P, Maris V, Wardle DA, Aronson J, Courchamp F, Galil B, García-Berthou E, Pascal M, Pyšek P, Sousa R, Tabacchi E, Vilà M (2013) Impacts of biological invasions: What's what and the way forward. Trends in Ecology and Evolution 28: 58–66. https://doi.org/10.1016/j.tree.2012.07.013

Stoll P, Prati D (2001) Intraspecific aggregation alters competitive interactions in experimental plant communities. Ecology 82: 319–327. https://doi.org/10.2307/2679862

Strauss SY, Lau JA, Carroll SP (2006) Evolutionary responses of natives to introduced species: what do introductions tell us about natural communities? Ecology Letters 9: 357–374. https://doi.org/10.1111/j.1461-0248.2005.00874.x

Svenning J-C, Gravel D, Holt RD, Schurr FM, Thuiller W, Münkemüller T, Schiffers KH, Dullinger S, Edwards TC, Hickler T, Higgins SI, Nabel JEMS, Pagel J, Normand S (2014) The influence of interspecific interactions on species range expansion rates. Ecography 37: 1198–1209. https://doi.org/10.1111/j.1600-0587.2013.00574.x

Thompson K, Davis MA (2011) Why research on traits of invasive plants tells us very little. Trends in Ecology and Evolution 26: 155–156. https://doi.org/10.1016/j.tree.2011.01.007

Thorpe AS, Aschehoug ET, Atwater DZ, Callaway RM (2011) Interactions among plants and evolution. Journal of Ecology 99: 729–740. https://doi.org/10.1111/j.1365-2745.2011.01802.x

Vilà M, Weiner J (2004) Are invasive plant species better competitors than native plant species? – Evidence from pair-wise experiments. Oikos 105: 229–238. https://doi.org/10.1111/j.0030-1299.2004.12682.x

Wang P, Stieglitz T, Zhou DW, Cahill Jr JF (2010) Are competitive effect and response two sides of the same coin, or fundamentally different? Functional Ecology 24: 196–207. https://doi.org/10.1111/j.1365-2435.2009.01612.x

Williamson M, Dehnen-Schmutz K, Kühn I, Hill M, Klotz S, Milbau A, Stout J, Pyšek P (2009) The distribution of range sizes of native and alien plants in four European countries and the effects of residence time. Diversity and Distributions 15: 158–166. https://doi.org/10.1111/j.1472-4642.2008.00528.x

Wilson JRU, García-Díaz P, Cassey P, Richardson DM, Pyšek P, Blackburn TM (2016) Biological invasions and natural colonisations are different – the need for invasion science. NeoBiota 31: 87–98. https://doi.org/10.3897/neobiota.31.9185

Zając M, Zając A, Tokarska-Guzik B (2009) Extinct and endangered archaeophytes and the dynamics of their diversity in Poland. Biodiversity: Research and Conservation 13: 17–24. https://doi.org/10.2478/v10119-009-0004-4

Zhang Z, van Kleunen M (2019) Common alien plants are more competitive than rare natives but not than common natives. Ecology Letters 22: 1378–1386. https://doi.org/10.1111/ele.13320

Supplementary material 1

Supplementary materials

Authors: Christine S. Sheppard, Marco R. Brendel

Data type: tables, figures

Explanation note: **Appendix 1.** Establishment of targets and neighbours. **Table S1.** The 47 Asteraceae species used in the experiment. **Table S2.** Linear regressions of species-specific competitive effects of neighbours on the five native target species. **Figure S1.** Alien-native continuum of the 47 Asteraceae species. **Figure S2.** Target biomass depending on neighbour species in the nutrient-poor soil. **Figure S3.** Effects of neighbour biomass on target performance in the control analysis.

Copyright notice: This dataset is made available under the Open Database License (http://opendatacommons.org/licenses/odbl/1.0/). The Open Database License (ODbL) is a license agreement intended to allow users to freely share, modify, and use this Dataset while maintaining this same freedom for others, provided that the original source and author(s) are credited.

Link: https://doi.org/10.3897/neobiota.65.63179.suppl1